7.—The Cheek-teeth of Hypsiprymnodon moschatus Ramsay 1876 (Macropodidae: Marsupialia)

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The morphology of the cheek-teeth and their replacement in *Hypsiprymnodon moschatus* is described. The cusps of the unworn lower deciduous molariform premolar and the first molar indicate that the problem of cusp homologies of the lower molars of Macropodidae is more complex than originally believed. A better understanding of the homologies of the parts of the lophodont molars is achieved, e.g. the antero-basal-cingulum of some authors is the homologue of the basin of the trigonid.

Introduction

Hypsiprymnodon moschatus, the Musk-Kanga-oo of Queensland, is the smallest of the Macro-odidae and is also in some respects the most rimitive of them. In spite of the phylogenetic nterest which is attached to it, the implications o be derived from the morphology of its eciduous teeth are not understood.

In the collection of the National Museum of ictoria, Melbourne, there is an extremely fine ut small series of skulls of this species which lustrates dental replacement. This series is escribed here. From it, it is established that ne third premolars are fully sectorial teeth hich only differ from the fourth premolars in ze and in the number of transverse ridges hich are on them. In this respect *Hypsiprym-odon* is not transitional between Phalangeridae nd Macropodidae. However, the deciduous remolars (milk-molars) are less molarised an in other Macropodidae (except *Potorous atyops*) and throw much light on the cusp omologies of the succeeding molars. The ructure of the maxillary teeth of *H. moschatus* so appears to lend support to Butler's theory the action of gradient fields along the length the developing tooth row.

Material

.M.V. No. R4598 (Fig. 1a; Fig. 2a; Plate 1, Figs. 1 & 2) ♀ Locality, date of collection, and collector unknown. General description: Juvenile with third premolar fully erupted, succeeded by maxillary teeth to the second molar which is only just visible. The second upper incisor is fully erupted, while the first and third upper incisors and the canines are only partly erupted.

.M.V. No. R5449 (Fig. 1b; Fig. 2b; Plate 1, Fig. 3) Sex unknown. Locality—Evelyn Scrub, North Queensland. Date of collection unknown. General description: The permanent premolar has replaced the milk-molar but the third premolar in front of it is still in position.

N.M.V. No. R4697 Adult ♀ from Lake Eacham, North Queensland, 2,300 feet, 21.5.11. Collector "G.S." General description: Teeth fully erupted but relatively unworn.

Description

Maxillary Teeth

R.4598. (Fig. 1a; Plate 1, Fig. 1)

P^3. The third upper premolar is a specialised sectorial tooth with a longitudinal median ridge which forms its cutting edge. The front of the tooth is slightly tilted outwards so that the axis of this ridge is at a small angle to the main longitudinal axis of the molar toothrow. Five transverse crests cross this ridge and, at the points where they do so, the ridge is raised into cusps so that the cutting edge of the tooth is serrated. The tooth appears to be three-rooted.

dP^4. The milk-molar (or deciduous fourth premolar) has three main cusps. The main longitudinal axis of the tooth is marked by a continuous longitudinal crest which is made up of the antero-posterior ridges of the two main cusps of the tooth which are thus united. The longitudinal crest is not functionally continuous with that of P^3 in front of it, but it is slightly displaced buccalwards. However, that part of the crest closest to P^3 (the median anterior ridge of the paracone) is parallel to the longitudinal crest of P^3. At the front of dP^4 this crest bifurcates and is continued back along both sides of the tooth as a cingulum. On the lingual surface the cingulum is well-marked, cuspidate, and finally becomes continuous once more with the posterior end of the main longitudinal crest (the median posterior ridge of the metacone). On the buccal surface of the tooth, the cingulum is less well-marked and, posterior to the level of the paracone, it is no longer visible. The main cusps are well-marked. The paracone, which rises very close to the centre of the tooth, forms the highest part of the median longitudinal crest. The metacone lies behind it, close to the posterior edge of the tooth and, strangely, it appears to lie slightly to the lingual side of the median longitudinal crest so that there is a distinct kink in the ridge where it turns to ascend to the tip of the cusp. The protocone is a distinct cusp situated about midway along the lingual cingulum; there is a small cingular cuspule anterior to this, and

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in front of this cuspule the cingulum becomes functionally continuous with the median longitudinal crest of P^3. Behind the protocone there is a well-marked cingular cusp mesial to the metacone. This is almost certainly the hypocone.

M^1. The first molar is quadritubercular and, unlike the condition in the tooth in front of it, the four major cusps form two more-or-less parallel longitudinal crests of equal (but not constant) height. The lingual one is functionally continuous with the posterior part of the lingual cingulum of dP^4, and is clearly its homologue, while the buccal one is functionally continuous with the median longitudinal crest of dP^4. The tooth, in comparison to dP^4, is shortened in front of the paracone; this gives it a rather oblong shape. M^1 has all the cusps of dP^4, but their size relations are different—in addition one new cusp has appeared. This new cusp is on the anterior ridge of the paracone where it sweeps down to become continuous with the cingulum. As in dP^4, the lingual cingulum is continuous but on it the protocone and hypocone are so enlarged that it is as high as the other longitudinal crest which lies buccal to it; the hypocone is even higher than the metacone which lies lateral to it. As in dP^4, the metacone is clearly set off from the longitudinal crest and is connected with it by a slight transverse ridge.

M^2. In this specimen the second molar is just visible in its alveolus and it appears to be very much like M^1. The main differences are that the cingular cuspule on the anterior slope of the protocone is not present, and that the apex

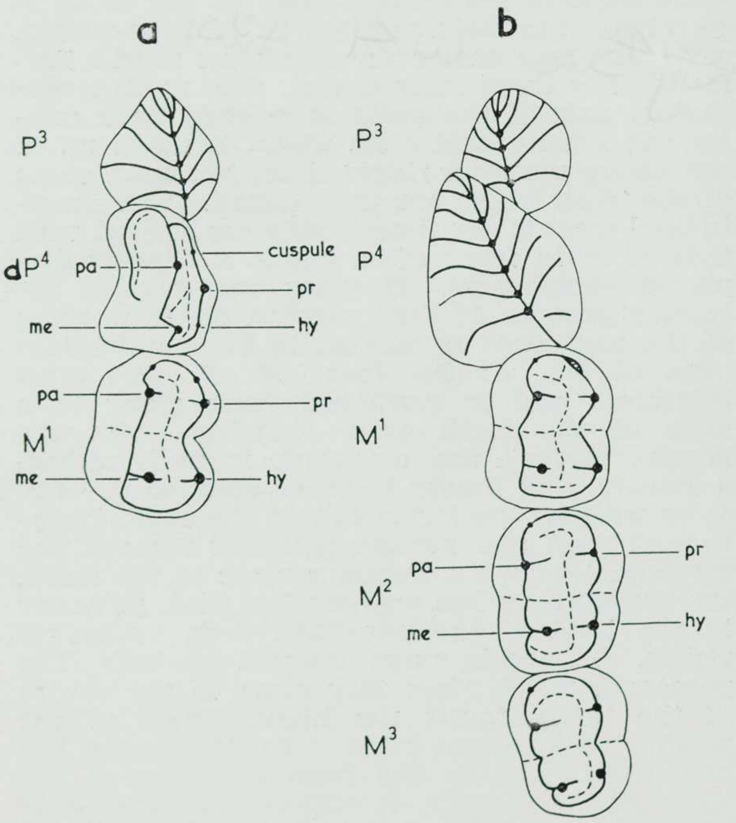


Fig. 1.—Right maxillary tooth-rows of *Hypsiprymnodon moschatus* (a) R4598, (b) R5449. Unerupted teeth not shown. Buccal side towards the left of the page. Abbreviations: pa. paracone, me. metacone, pr. protocone, hy. hypocone. Ridges and crests shown by continuous lines, bottom of valleys by broken lines.

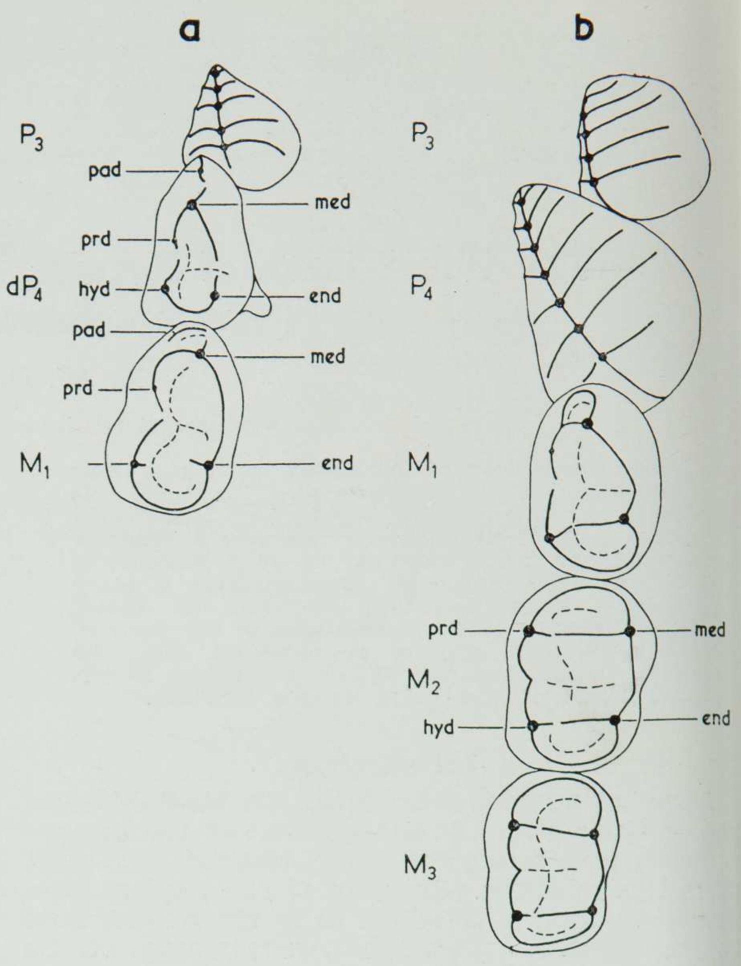


Fig. 2.—Mandibular tooth-rows of *Hypsiprymnodon moschatus* (a) R4598, right row reversed, (b) R5449, left row. Unerupted teeth not shown. Buccal side towards the left of the page. Abbreviations: prd. protoconid, med. metaconid, pad. paraconid, hyd. hypoconid, end. entoconid. Ridges and crests shown by continuous lines, bottoms of valleys by broken lines.

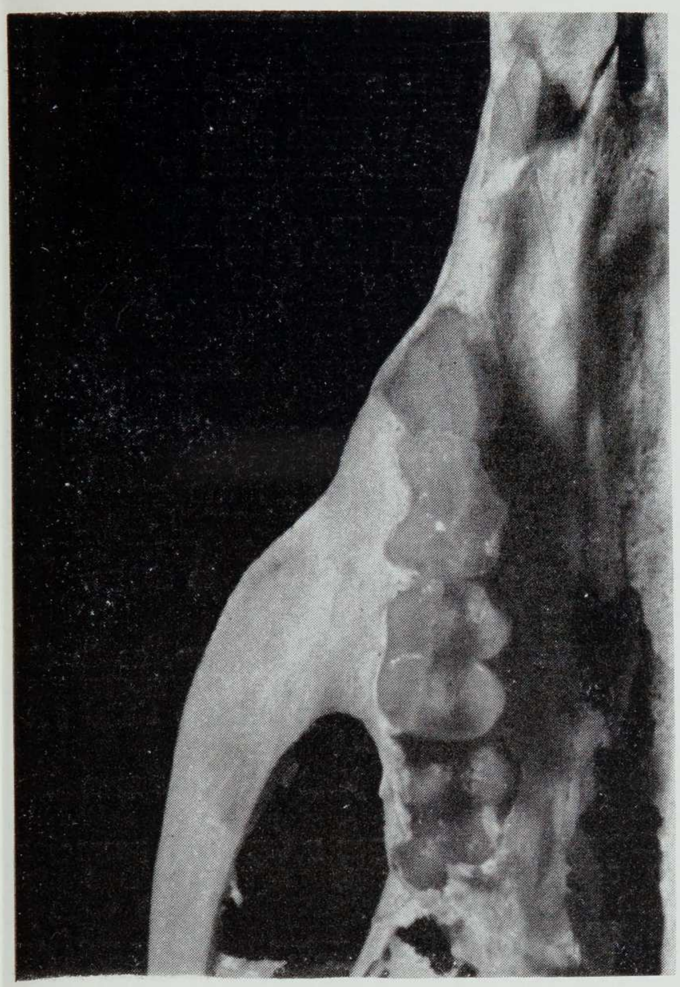
of the paracone (rather like that of the metacone) is also slightly set off to the lingual side of the buccal longitudinal crest.

R.5449. (Fig. 1b.)

In this specimen P^4 has replaced dP^4 but P^3 has not been shed. P^3 is in all respects similar to that described in R4598.

P^4. This sectorial is larger than P^3 and the angle between its median longitudinal crest and the main axis of the tooth-row is greater (i.e. it is more sharply out-turned). Further, six transverse crests cross the longitudinal crest instead of five. On the postero-lingual surface of the tooth a seventh ridge runs up to the median longitudinal crest but fades away before it reaches it. It would appear to be directed to a point slightly to the rear of the cuspule formed where the sixth transverse ridge and the longitudinal ridge intersects.

M^1. In this specimen (in which tooth replacement has taken place) it is now clear that the small cingular cuspule anterior to the protocone is functionally related to the median longitudinal crest of P^4 in the same way as its homologue in dP^4 is to the median crest of P^3. In this specimen the cuspule has already become worn and is scarcely discernible on the antero-lingual slope of the protocone; a well-marked wear-facet almost obliterates it. This facet also runs on to the posterolingual face of P^4.



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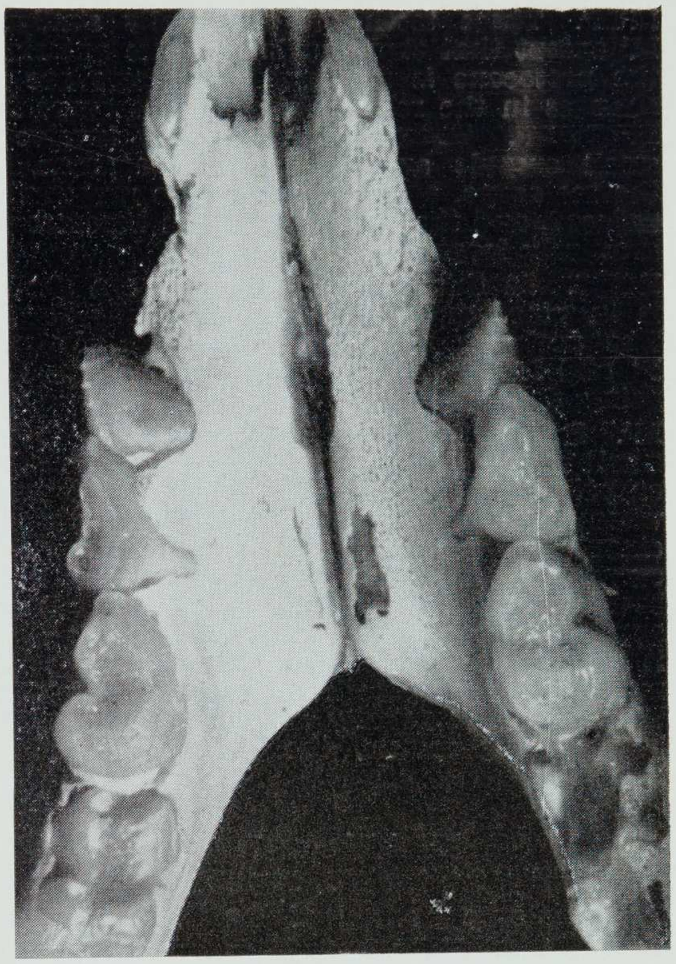

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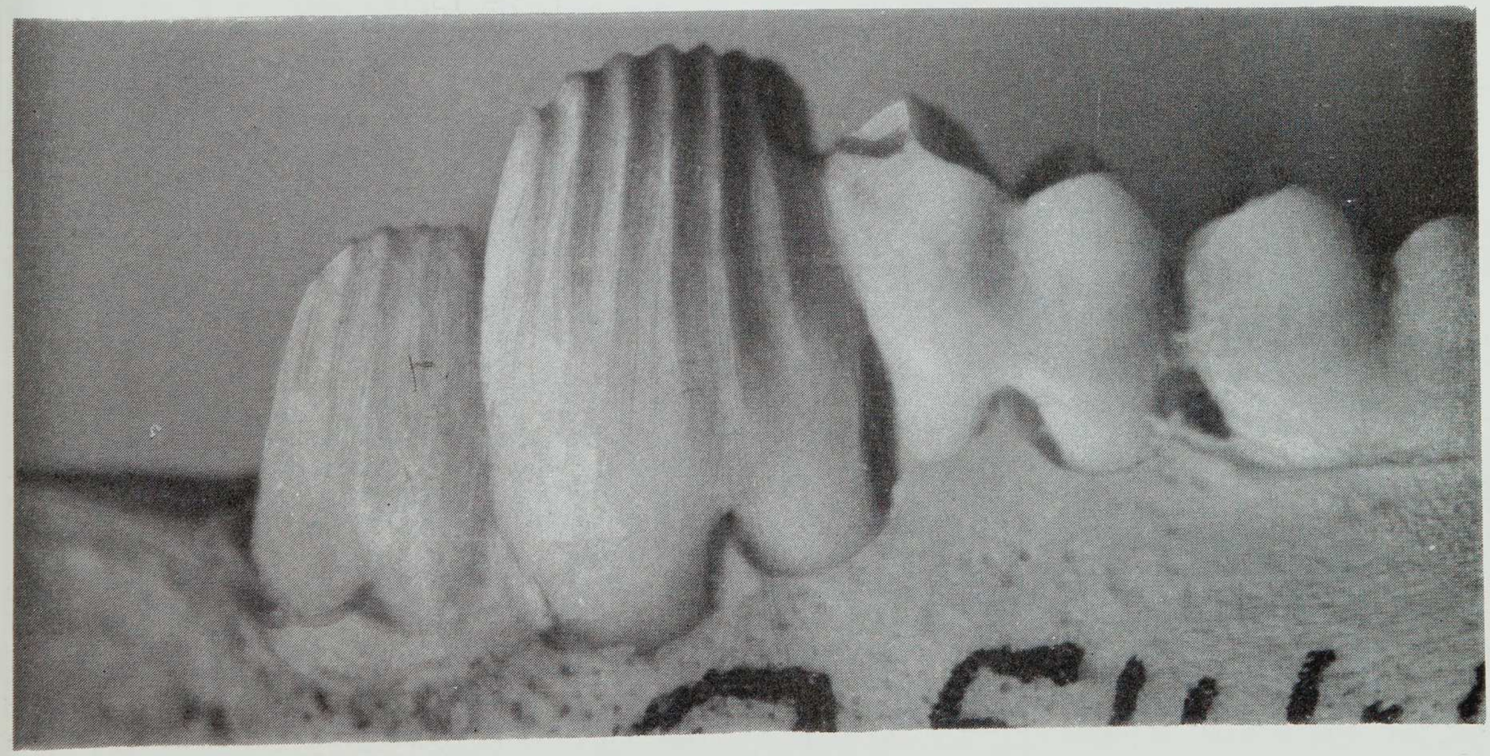

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PLATE I

Fig. 1.—Right maxilla of R4598.

Fig. 2.—Mandibular tooth-rows of R4598. Left M^2 exposed in alveolus, undissected on right. The thin bone at the posterior end of the mandibular symphysis has broken away exposing the root of the developing incisor.

Fig. 3.—Left lower premolars of R5449. P_3 and P_4 are both in place and are morphologically similar. Photograph taken of buccal surface.

M^2M^3. These teeth are essentially similar to M^1 except that the cingular cuspule anterior to the protocone is not present. There are also changes in the relative sizes of the cusps from M^1 to M^3. These changes mainly involve the small cuspule anterior to the paracone, and the metacone, which both become progressively reduced, and the protocone which becomes progressively larger.

R4697. In this specimen P^3 has been shed. P^4 is in place and all molars are fully erupted. The posterior molars are only slightly worn. P^4 and M^{1-3} add nothing further to the foregoing descriptions.

M^4. In the last molar the metacone is very small indeed being little more than a raised cuspule on the posterior crest of the paracone where it sweeps round to become the posterior cingulum. The trend in the reduction of the cuspule anterior to the paracone which has been described in M^{1-3} has stopped and it even appears to be slightly larger than that of M^3, it appears to be anterobuccally displaced. The main cusp of the tooth is clearly the protocone. The tooth is essentially tricuspid the main cusps being the paracone, the protocone, and the hypocone.

Mandibular Teeth

R4598 (Fig. 2a; Plate 1, Fig. 2)

P_3. The cusp pattern of the third lower premolar is the same as that of its upper homologue. There is a similar longitudinal crest with five transverse crests; there are raised cuspules where these intersect.

dP_4. The lower milk-molar is a tooth which is shaped like a wedge with the apex directed anteriorly. The trigonid is compressed. Its main cutting crest runs obliquely from the anterior-buccal-face to the lingual surface of the tooth which it reaches before the commencement of the talonid. This crest is parallel with that of P_3 but is not functionally continuous with it. The metaconid is by far the largest cusp of the tooth and is the main contributor to the functional crest. The paraconid is a small but distinct cuspule on the antero-buccal slope of the ridge of the metaconid. From the buccal side of the apex of the metaconid a small crest descends and sweeps backwards as far as the buccal edge of the valley which runs transversely across the tooth between the trigonid and talonid. Just before this small crest reaches the bottom of the valley, it is interrupted by a raised cuspule. This is clearly the protoconid since it only differs in size from that cusp on the succeeding tooth (and the protoconid of M_{2-4} of other specimens). The talonid has a marginal crest which is slightly raised into cusps in two places. One of these elevated cusps is buccal (the hypoconid) and the other lingual (the entoconid).

M_1. The talonid of the first lower molar is considerably enlarged and its cusps are widely separate as compared with those of dP_4. The trigonid is about the same size as that of dP_4, but the posterior part of the tooth is so much larger that the anterior part of the trigonid appears minute by comparison. The valley between paraconid and metaconid is deepened and broadened behind the laterally-widened paraconid; this transversely placed cusp and the valley behind it thus appear as a small fosette anterior to the metaconid. The ridge which bears the protoconid is much more distinct than it was in dP_4 but the protoconid is still little more than an eminence which is raised slightly above it. The two cusps of the talonid stand well above the general level of its marginal crest and are both nearly as high as the metaconid which is no longer the only really large cusp as it was in dP_4. From both the entoconid and the hypoconid, low ridges run transversely down into the basin of the talonid.

M_2. In this specimen the second lower molar is scarcely visible in its alveolus and, from what can be seen, it appears that the protoconid, paraconid, hypoconid, and entoconid are more-or-less equal in height and are set opposite each other so that the tooth is oblong in shape.

R5449. (Fig. 2b; Plate 1, Fig. 3.)

In the mandible of this specimen, as in the maxilla, the permanent premolar has replaced its milk predecessor. Here, too, the third premolar is still in position.

P_3. Is identical with that of specimen No. R4598.

P_4. Here as in the upper permanent premolar, there are seven transverse ridges but the seventh is rather better developed so that it reaches and crosses the longitudinal crest. As in the case of the other six, there is a small cuspule at the point at which they intersect.

M_1. The first lower molar is like that already described for R4598, but there is a somewhat greater development of the ridge which runs away from the apex of the entoconid towards the hypoconid. In the centre of the basin of the talonid this meets a similarly developed ridge from the hypoconid. This transverse crest cuts off the posterior part of the basin of the talonid from the median longitudinal valley of the tooth so that a small posterior fossa is formed at the back of it. This is bounded posteriorly by the marginal crest which runs round the back of the tooth between hypoconid and entoconid (see description of dP_4 in R4598).

M_2. In the second lower molar, the protoconid is as high as the entoconid and the hypoconid; further, it is displaced buccalwards so that there is now a wide space between it and the metaconid. It will be remembered that in dP_4 the protoconid is little more than an elevation on a crest which swept around the front of the tooth, first buccalwards, then posteriorly from the tip of the metaconid. In M_2 the crest still remains but it has here become greatly depressed between protoconid and metaconid so that it is now made up of two separate ridges which meet in the bottom of the median valley of the tooth. These crests run transversely from the apices of their respective cusps (protoconid and metaconid) down into the median longitudinal valley. This valley runs antero-posteriorly down the centre of the tooth and is only broken where the transverse ridges from the protoconid and the metaconid, and from hypoconid and entoconid, meet. The paraconid has now disappeared and the ridge, which in dP_4 was the anterobuccal ridge, now sweeps down from the metaconid around the front of the tooth and up to the apex of the protoconid. The tooth is now a typical macropod molar with two transverse lophs (here somewhat depressed between the cusps) and an anterior "shelf," or "anterior basal cingulum" (actually the basin of the trigonid with the paraconid depressed) and a "posterior fossa" (actually the cut-off posterior part of the basin of the talonid).

M_3. The third molar is smaller than the second but otherwise not different in form from it.

M_4. This tooth is just visible in its alveolus.

R4677.

M_4. The last lower molar is smaller than M_3 but is otherwise morphologically similar to it.

Discussion

Maxillary Teeth

This small but excellent series of *Hypsiprymnodon* establishes that the third and fourth premolars are both more highly specialized as sectorials than those of most other Macropodidae. Like *Bettongia,* P^3 is as specialized as P^4 and only differs from it in its rather smaller size and less number of grooves. Some species somewhat closely related to *Bettongia,* e.g. *P. platyops,* are much less specialized in this respect, as was the specimen of *Hypsiprymnodon* figured by Carlsson (1915, Plate 2, Figs. 12-15), where P^3 is shown to be a five cusped tooth without the extreme sectorial specialization of P^4. Tate (1948, p. 244) made Carlsson's statement the basis of his remark that the difference between P^3 and P^4 of *Hypsiprymnodon* is greater than in all Macropodidae. In my discussion of the form of the cheek-tooth row in Macropodidae (Ride 1956, p. 423) I drew attention to Carlsson's description and stated that *Hypsiprymnodon* was an exception (and by inference more primitive) to the general rule that macropods possess, at all stages of growth, a row of cheek-teeth which comprises a sectorial premolar followed by molariform teeth (i.e. P3 sectorial, dP4 molariform, M1-4 molariform or P4 sectorial, M1-4 molariform). Some species depart from this in late life when anterior teeth have become shed and the sectorial lost.

Wood (1960), in a paper received while this paper was in press, has shown that P^3 of *Hypsiprymnodon* is sectorial as in other Macropodidae and that Carlsson had mistaken dP^4 and M^1 for P^3 and dP^4.

In the single specimen of *Hypsiprymnodon* in the N.M.V. series which shows the process of tooth replacement (R5449) it is seen to be atypical of Macropodidae since only dP^4 is replaced. P^3 is presumably shed later. Wood (1960) found this in his material.

Although both permanent premolars (P^3 and P^4) are more specialized than those of most other Macropodidae, the milk-molar (or deciduous premolar) dP^4 is less molariform than that of all other genera of this family known to me, with the possible exception of some *Potorous*. The only skull of *Potorous platyops* in the collection of the Western Australian Museum has a worn dP^4 which appears to indicate that this species may be as unspecialized as *H. moschatus* in this respect.

Butler (1952*b*) has applied the theory of gradient fields to the development of the dental lamina in an attempt to understand the phenomenon of the progressive molarisation of milk molars which is so common a feature of the phylogeny of herbivorous mammals. He has argued (1952*b*, p. 838) that molarisation of the milk molars may be regarded as an extension forward in the dentition of the sphere of action of the ontogenetic factors that cause the dental rudiments to develop into molariform teeth. He suggested that, primitively, the molarising factors at the milk-molar level become modified before the ontogenetically-later permanent premolars develop. Thus permanent premolars appear as simplified (unmolarised) replacements of molariform teeth. However, in forms that are evolutionarily advanced in the development of molariform tooth-rows the action of molarising factors persists longer in the premolar region with the result that the permanent premolars also became molarised. Butler (1952*b*, p. 819) has pointed out premolars may be

TABLE I

Lengths of upper premolars of *Hypsiprymnodon moschatus* and relation between growth of the molar-row and premolar replacement.*

Number	N.M.V. R4598	N.M.V. R5449	N.M.V. R4697	N.M.V. R4597
Sex	♀	?	♀	?
P^3	2·5	2·4	....	....
dP^4	2·9	....	....	....
P^4	....	4·0	4·2	4·0
Stage of molar eruption	M^1 fully erupted	M^3 fully erupted	M^4 fully erupted (unworn)	M^4 fully erupted (worn)
Point in molar row opposite descending processes of zygomata	M^1 posterior loph	$M^{1/2}$ contact	$M^{1/2}$ contact	M^2 middle of tooth

* Crania were incomplete and basal length cannot be given Teeth were measured along the major axis of each tooth and only ename surfaces were included.

simpler in pattern than the deciduous teeth which they replace (hyposphyric) or they may even have the same patterns (isosphyric). He has shown that in the marsupial *Didelphis* the replacing premolar is hyposphyric (Butler 1939) and, in terms of molarizing factors and gradient fields in the developing dental lamina, that P^4 represents a much lower level on the molarization gradient than its ontogenetic predecessor (heteroclinous). However, in *Hypsiprymnodon* and other Macropodidae the permanent premolars P^3 and P^4 are so unlike the milk-molar (dP4) that additional modifying factors are clearly operating.

Sectorial premolars are developed in Phalangerinae (the group from which the Macropodidae are presumed to have evolved) but little is known of tooth replacement in them. In juvenile *Trichosurus vulpecula* P^3 is absent and only dP^4 is replaced by P^4. P^4 is a sectorial while dP^4 is a bicuspid, i.e. the molarization gradient has not reached dP^4.

Several groups of Phalangeridae have developed sectorials independently. In each of them the specialisation appears to be confined to the last premolar (P^4) while P^3 may be widely different from it or even absent. In the fossil form *Burramys parvus* the last premolar (P^4) is a serrated sectorial which is scarcely different from that of *Hypsiprymnodon moschatus* while P^3 is a small buttress-like nubbin (without cusps) which lies adpressed against its antero-lingual face (see Ride 1956). It would seem that nowhere among known Phalangeridae is there evidence of a gradient field of sectorial elaboration from the front to the rear of the tooth-row.

Bensley (1903, p. 147) recognised the probability that the evolution of sectorial premolars in Macropodidae was one of forward elaboration from the last permanent premolar (P^4). From the morphology of P^3 of *Hypsiprymnodon* it is now clear that *Hypsiprymnodon* is far from primitive in this respect; indeed, it is as specialized as *Bettongia*. This conclusion serves to emphasize the anomolous phylogenetic position of *Hypsiprymnodon*. It has been considered by many to be the most primitive of all Macropodidae and this is clearly true of some characters which it possesses, e.g. the hallux, digital pads in the pes, simple stomach, simple molars, scarcely molarized dP_4. In other directions however, it is clearly specialized to a greater extent than most Macropodinae e.g. possession of anterior-vaginal-expansions in the female urogenital system (see Pearson 1945, 1949*a* & 1949*b*), the degree of elaboration of P^3, and the contact between squamosal and frontal in the side of the braincase.

This study of cusps of the upper molars of *Hypsiprymnodon* supports the nomenclature which is conventionally applied to them in Macropodidae. In the milk-molar (dP^4) the paracone is the largest cusp and it can be serially traced down the molar series as the antero-external cusp. Further, it is likely that this is the primary cusp (see Butler 1956). The protocone and metacone are developed on the lingual cingulum. This supports Butler's (1941) contention that the protocone on the molariform teeth is serially homologous with the lingual cingulum of less molariform teeth.

A comparison of molar cusps from dP^4 backwards also adds probability to the hypothesis of the action of gradient fields in dental ontogeny. It seems that such features as the graded increase in size of the protocone from anterior to posterior teeth, and similar increase in size of the metacone to M^1 and then its subsequent reversion to small size in M^4 can best be explained in this way. There is, however, one cuspule on two of the upper teeth which can best be explained by means other than the operation of gradients. This is the cuspule on the anterior slope of the protocone dP^4 and M^1. In both teeth this cuspule is related in position to the functional cutting edge of the tooth in front of it in such a way as to provide continuity between the teeth. In the case of M^1 the cuspule is related both to the lingual cingulum of dP^4 (Fig. 1a) and to the median longitudinal crest of P^4 (Fig. 1b), although in the latter case the function does not persist long since its place is soon taken by a wear facet. It is of interest to compare this cuspule with those of *Burramys parvus* in which P^4 is similarly outwardly rotated and with *Dactylopsila trivirgata* in which the axis of P^4 is rotated in the opposite direction. In *Burramys parvus*, M^1 has a cuspule which is identical in position with that of *Hypsiprymnodon*, while in *Dactylopsila* an accessory cuspule is developed anterior to the paracone (see Ride 1956, p. 426 and Fig. 3). The development of these cuspules would appear to be related in some way to the shearing function of the crest of the tooth in front. Butler (1952*a*, p. 786, Fig. 5) illustrates parastyles on the milk-molars of Tapiroidea which are almost certainly of the same kind. Here, however, one can also discern a gradient of elaboration along the tooth-row much as the one that can be seen in the small cuspules on the anterior ridge of the paracone of the molars of *Hypsiprymnodon*.

Mandibular Teeth

The morphology of the lower molars and milk-molar of *H. moschatus* clearly supports the cusp-terminologies in use in the modern literature of the Phalangeroidea (e.g. Stirton 1957). Bensley (1903) appears to apply the same terminology to the posterior molars of Phalangerinae, Phascolarctinae and Macropodidae, but his reason for this is not clear since in his discussion of the morphology of M_1 of the Macropodidae he argues that the element which I consider to be a protoconid is actually a "protoconid-like" accessory cusp and my metaconid is actually the true protoconid. In particular, he states with reference to the potoroines *Bettongia* and *Aepyprymnus* (op. cit. p. 145) that the anterior lobe of M_1 "bears an accessory cusp on its outer slope. The new cusp takes up the position of a protoconid, but is obviously not homologous with that element, the true protoconid being the inner cusp, the true metaconid having been lost in the Phalangerine stage". If this view is correct, and if the four cusps of M_1 are the serial homologues of those of the teeth behind, then a new cusp terminology (different from that used by all present workers) is necessary for the posterior molars of Macropodidae. The alternative is to assume that dP_4 and M_1 have special patterns resulting from occlusal relations with P^3 and P^4 and that the positions of the "new" cusps which have developed on them are merely coincidentally those occupied by their non-homologues on M_{2-4}. The strongest argument in favour of this view is that the principal cusp of the lower teeth is the protoconid and it is surprising to find it reduced in the least molarized of the cheek teeth although such an occurrence might be expected further up the molar gradient.

This problem of interpretation of the homology of the cusps does not arise among Phalangerinae. When a reduction in the number of cusps of M_1 occurs (as it does in *Petaurus breviceps*), the two posterior cusps are clearly the entoconid and hypoconid, while the anterior cusp would appear (by comparison with M_2) to be the homologue of the antero-lingual cusp of the quadritubercular tooth, i.e. the metaconid. However, in less-specialized Phalangerinae (e.g. *Trichosurus vulpecula*) M_1 is quadritubercular and the cusp which is missing on that tooth in *Petaurus* is present although somewhat reduced. The reduced cusp is the metaconid and the larger protoconid stands close to it, being somewhat lingually displaced, so that the isolated anterolingual cusp of *Petaurus* is clearly the protoconid in spite of its apparent correspondence with the metaconid of the succeeding tooth.

In the Phascolarctinae, a problem of interpretation like that in *Hypsiprymnodon* occurs. In *Pseudocheirus* one of the anterior cusps of M_1 is reduced, and here I believe that it is the protoconid which is reduced while the metaconid is enlarged.

Bensley (1903, p. 137) interpreted the M_1 of Phascolarctinae and Phalangerinae as I have done but, in addition, he mentioned that an alternative interpretation would be to consider the antero-buccal cusp of the phascolarctine M_1 a new accessory cusp and the large antero-lingual cusp the true protoconid—the metaconid having disappeared. If this latter interpretation is correct, the protoconid would be the antero-lingual cusp of the phascolarctine M_1; again the succeeding lower molars have the same number of cusps in almost identical positions and these are also presumably the serial homologues of those of M_1.

In conclusion, if the principle of the serial homology of cusps occupying similar positions on successive teeth in the molar row be accepted, then the logical outcome of these interpretations of M_1 (which differ from those employed in this paper) is that the protoconid of the succeeding molars is antero-buccal in Phalangerinae, while it is antero-lingual in Phascolarctinae and *Hypsiprymnodon* (and presumably in all Macropodidae). Since Macropodidae are commonly held to be more closely related to Phalangerinae than to Phascolarctinae, this can only be regarded as unlikely.

From Bensley's account it is clear why he considered that evidence existed of the loss of the metaconid in primitive Macropodidae. In his description of the M_1 of *Hypsiprymnodon* (p. 144) he stated that "as in the advanced Phalangerinae, the first lower molar has but one cusp on its anterior lobe". Bensley clearly had no specimen of *Hypsiprymnodon* with dP_4 or with unworn M_1 and he did not observe the small protoconid.

There is no evidence that the first molar of Macropodidae has ever been other than four cusped, and there is certainly no evidence that the ancestral form possessed a three cusped tooth like that found in some small Phalangerinae today. The almost three cusped M_1 of *Hypsiprymnodon* is convergent upon that of *Petaurus* and similarity is achieved by the loss of different elements.

The condition of the partly molarised M_1 and dP_4 are of great help in understanding the homologies of the parts of the lophodont molars of more typical Macropodinae. From these it is clear that the so-called "antero-basal cingulum" of the macropodine lower molar is the homologue of the basin of the trigonid.

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